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## **Teaching and curiosity: sequential drivers of cumulative cultural evolution in the hominin lineage**

van Schaik, Carel P ; Pradhan, Gauri R ; Tennie, Claudio

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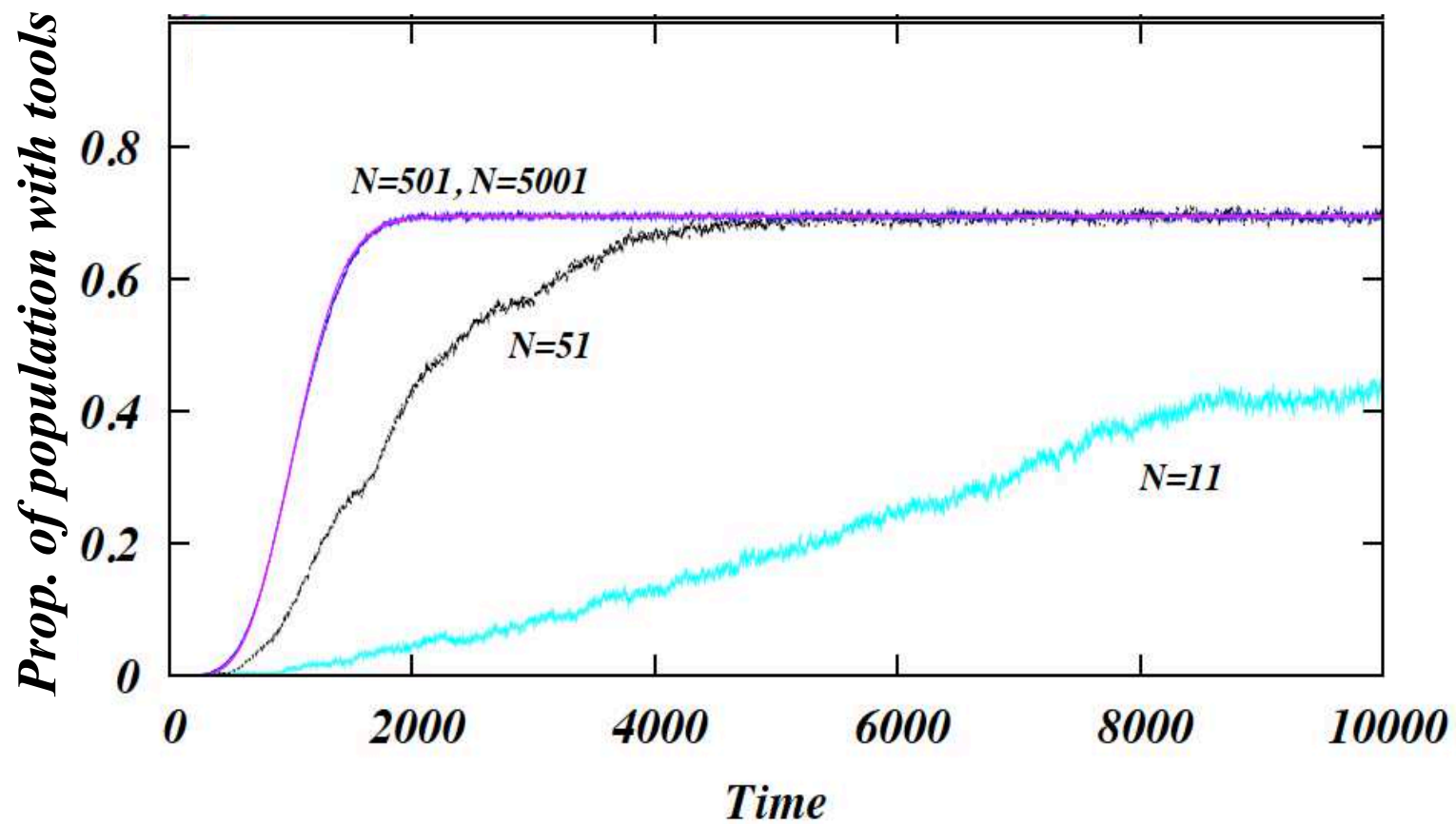
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# Behavioral Ecology and Sociobiology

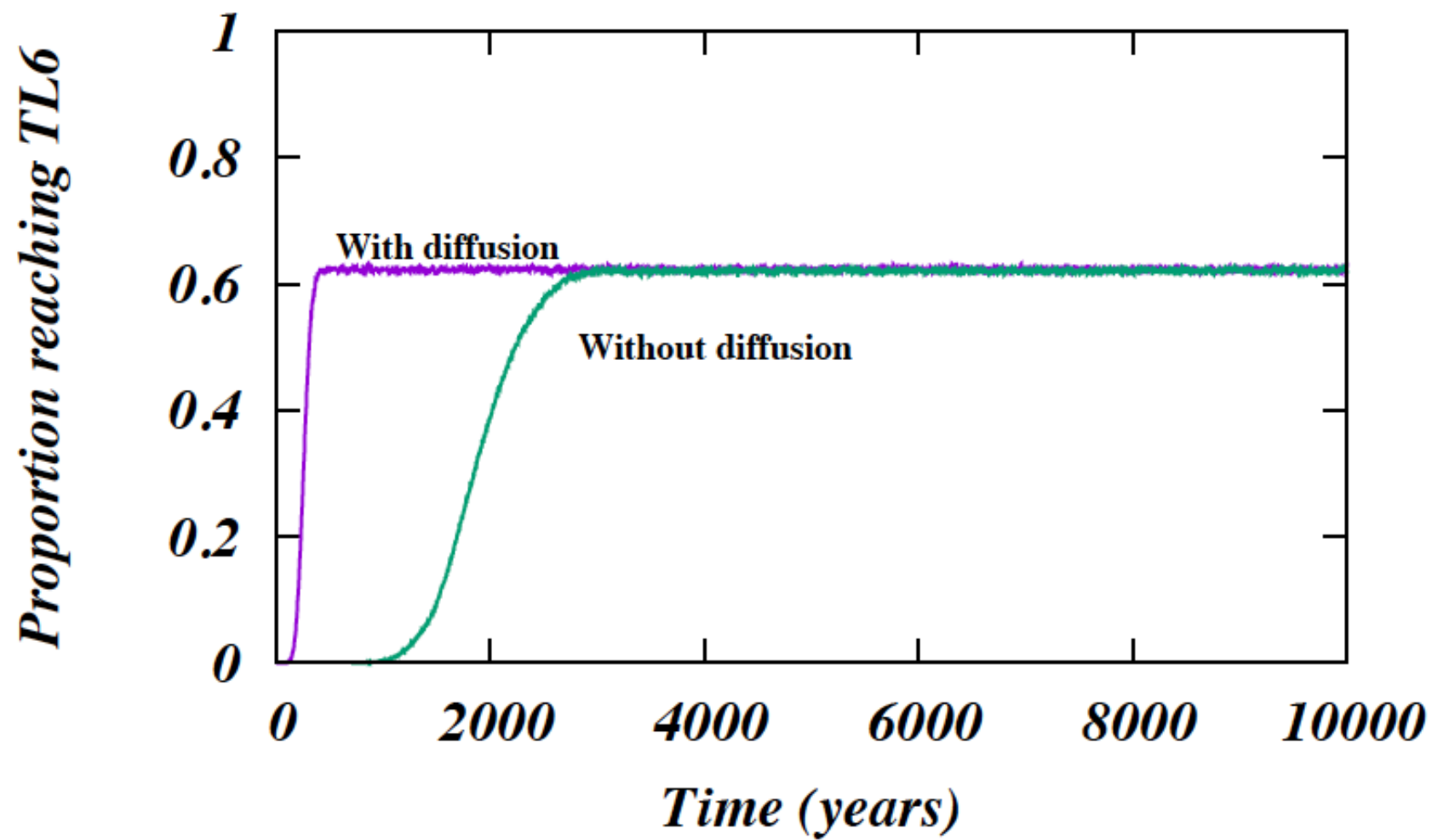
## Teaching and Curiosity: sequential drivers of cumulative cultural evolution in the hominin lineage --Manuscript Draft--

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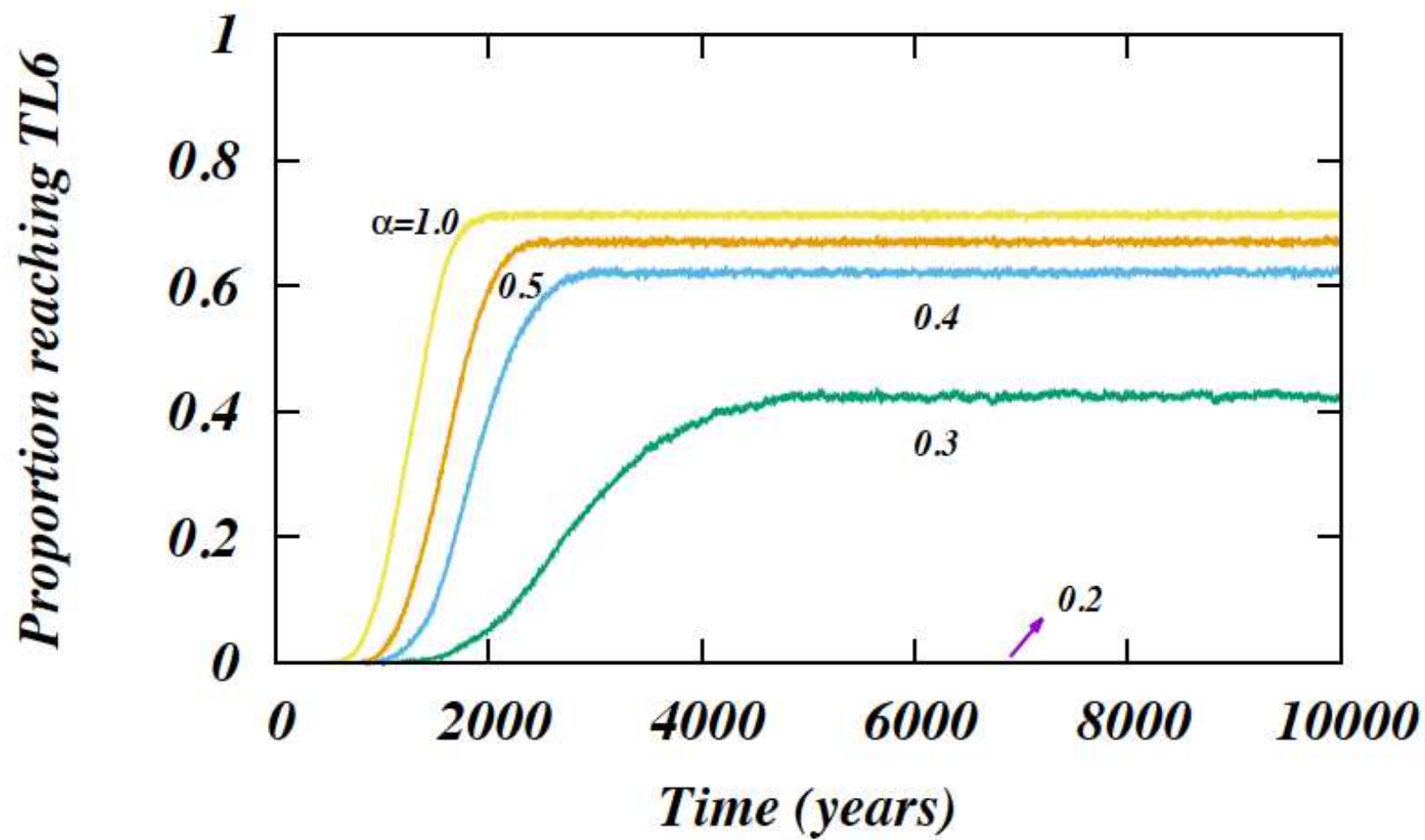
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Figure



Figure



**Table 1**

The major leaps in the pace of cultural evolution during human evolution

Major transition	When?	Major driver
<i>Homo heidelbergensis</i>	after 500 ka	<b><i>Intensive cooperation</i></b> : involving use of language and teaching of young, both driven by extensive allomaternal care and systematic food sharing.
<i>Out-of-Africa</i>	ca 75 ka	<b><i>Curiosity unleashed</i></b> : sudden failure of regular foraging, leading to need to invent new resource exploitation methods, leading to novel niche dimensions.
<i>Neolithic</i>	ca 10 ka	<b><i>Incentives for specialization</i></b> : after development of sedentism and then agriculture, producing increased incentives to innovate, due to private benefits from specialization and trade, and need for effective wars.

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8 **Teaching and Curiosity: sequential drivers of cumulative cultural**  
9 **evolution in the hominin lineage**

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26 **Abstract**

Many animals, and in particular great apes, show evidence of culture, in the sense of having multiple innovations in multiple domains that are influenced by social learning. But only humans show strong evidence of complex, cumulative culture, which is the product of copying and the resulting effect of cumulative cultural evolution. The reasons for this increase in complexity have recently become the subject of extensive debate. Here, we examine these reasons, relying on both comparative and paleoarcheological data. The currently best-supported inference is that culture began to be truly cumulative (and so, outside the primate range) around 500,000 years ago. We suggest that the best explanation for its onset is the emergence of verbal teaching, which requires language and thus probably coevolved with the latter's evolution but also reflects the overall increase in proactive cooperation due to extensive allomaternal care. Imitation, often considered critical, can emerge developmentally in ape-like primates once learned skills are too complex to be easily innovated independently. A subsequent steep increase in cumulative culture, roughly 75 ka, may reflect the rise of active novelty seeking (curiosity), which led to a dramatic range expansion and steep increase in the diversity and complexity of material culture. A final, and continuing, period of acceleration began with the Neolithic (agricultural) revolution.

**Keywords:** cumulative culture; stone tools; Out of Africa; imitation; verbal instruction; teaching



52

53

## 54 **Introduction**

55       Many animals show evidence of social learning, some show  
56 traditions, and a subset of these show multiple traditions in a range of  
57 domains, ranging from subsistence to comfort behaviors and  
58 communication, which also tend to be geographically variable (Whiten et  
59 al. 2017). Whiten and van Schaik (2007) proposed to reserve the term  
60 culture for the latter level of variation. These cultures generally consist of  
61 innovations that, once arisen, increase in frequencies via social learning  
62 until stopped by a dispersal barrier, which helps create geographic  
63 variation. However, variation may in some cases also be helped by social  
64 pressure to be similar to others (e.g. Luncz and Boesch 2014; van de Waal  
65 et al. 2017).

66       Despite the ubiquity of animal cultures, there is very little evidence  
67 (apart from the vocal domain, such as some bird and whale songs) for such  
68 cultures to be cumulative. A cumulative innovation is one that has a history  
69 of repeated copying plus modification of earlier forms, usually by addition  
70 (called ‘ratcheting’ by Tomasello et al. 1993). The paradigmatic case of a  
71 cumulative cultural effect is when an individual adds a technique used in a  
72 very different context or an entirely novel one to an existing (copied) one,  
73 and integrates the two functionally into a new technique. Cumulative  
74 culture is therefore culture that may become more complex over time as a  
75 result of the cumulation of modifications (we use this neologism to  
76 distinguish it from the more general accumulation, which refers to

increased cultural diversity: Dean et al. 2014). Some primate technology consists of several subparts and has thus been proposed to be cumulative (e.g., Sanz and Morgan 2007). Even so, while it is cumulative in that we see compound innovations, it is as yet unclear whether it meets another frequently used definition of cumulative culture (Boyd and Richerson 1996), i.e. that a naive individual could not independently innovate the more complex variants within its lifetime. In the following we will assume that chimpanzees, and other non-human great apes, do not have cumulative culture in this stronger sense (for a more in-depth review of the matter, see Tennie et al. 2018).

That human culture is cumulative and thus complex for both the material and institutional components is in fact one of the key differences between human and nonhuman cultures. Thus, most of us use technology every day that we could not have invented from scratch and that are the product of long process of cumulating modifications. While the study of cultural evolution in humans has become a thriving enterprise (Mesoudi 2016), explanations for the origin of this complexity remain elusive. The most popular idea is that cumulative culture became possible once humans evolved sophisticated imitation abilities and also teaching (Galef 1992; Tomasello 1999; Tennie et al. 2009; Lewis and Laland 2012), i.e. when they were able to pass on copies. However, when and why this happened during hominin evolution remains unresolved, despite increasing interest by behavioral biologists and psychologists (e.g. Dean et al. 2014; Kempe et al. 2014; van Schaik 2016; Laland 2017; Tennie et al. 2017).

101           The first hurdle is that the moment hominin technology became  
102 based on copying was not specified. By default, there is a widespread  
103 (though rarely made explicit) assumption that the smoking gun of copying  
104 can be seen in the origin of any (and thus lithic) technology in the record  
105 (Foley and Lahr 2003), although this assumption chose to treat as  
106 irrelevant obvious cases of tool use in the animal kingdom not usually seen  
107 as a product of cumulative culture (beaver dams, bird nests etc.). And so,  
108 cumulative culture was often, and thus tellingly implicitly, assumed to have  
109 started with the onset of the Oldowan at 2.6 Ma or perhaps even with what  
110 has been called the Lomekwian at 3.3 Ma (Harmand et al. 2015). This early  
111 start has rarely been questioned, but counterarguments are on the rise. For  
112 example, Tennie et al. (2016, 2017), partly drawing on great ape  
113 observations, suggested a far more recent origin of cumulative technology  
114 (at the earliest in the Acheulean, but probably later). We will accept this  
115 assessment here, but also delineate two subsequent periods of accelerated  
116 increases in complexity and evaluate hypotheses to explain them.

117           At the current state of knowledge, any conclusions will have to  
118 remain tentative. Nonetheless, the value of this approach is that integrating  
119 information from living animals encourages us to consider individual,  
120 social and demographic variables that are not always taken into account.

## 123   **The origin and rise of cumulative culture**

124           In this section, we examine the timing of the first clear signs of  
125 cumulative cultural evolution during hominin evolution (and thus of

cultural complexity beyond the range of extant great apes) and of subsequent periods of apparent acceleration in the cumulation process.

Wild great apes produce innovations via others through social-learning mechanisms that largely amount to socially mediated serial reinnovations (Bandini and Tennie 2017), and so innovations, even if occasionally consisting of several steps, nevertheless remain within the species' zone of latent solutions (Tennie et al. 2009), i.e. the set of innovations that individuals of the species can in principle independently invent during their lifetime. As a result, cultural repertoires of populations may come to differ (in the interplay between environmental and genetic differences, together with socially mediated reinnovations). However, while they may increase in diversity, they tend not to increase in complexity: there is no clear ratcheting (Tomasello 1999; Boyd and Richerson 1996).

Tennie et al. (2016, 2017) argued that our ancestors (hominins) engaged in the same thing (socially mediated reinnovation) for most of their existence. The record of our early stone-tool making ancestors reveals hundreds of thousands of years of stasis (variance exists, but around a mean) in both the Oldowan and Acheulean industries, which is unlikely if they really had represented cumulative culture (i.e. the passing on of actual copies of variants which automatically would have led to variants outside the relevant species' respective zones of latent solutions). This does not require that the ability to produce these technologies was genetically based in the sense of being developmentally strongly canalized (a view taken by Corbey et al. 2016), but that it was more likely cultural in

the same sense that extant primate technology is, relying on some form of social learning and socially induced individual practice (Schuppli et al. 2016). But if the practice part receives no social inputs that provide guidance over and above what the individual will likely converge on, and if no (or not enough, or too rarely) details are copied, i.e. if there is neither teaching nor imitation able to lead to *copies*, there will be a limit on the level of complexity that is achieved. Though of course, depending on factors such as a species' cognition and anatomy, concrete goals, raw material selectivity, ecological dependence on stone tools, life history (esp. maximum age) and perhaps most importantly, individual practice, the results would always show variability. But they would lack (as they do) a *fast* direction (the latter the hallmark of cumulative culture; compare Kempe et al. 2012).

With the origin of the prepared-core or mode-3 technology (grading into the Middle Stone Age), we see the emergence of even more complex tools, and with it a major leap in efficiency (cf. Muller and Clarkson 2016). We place this origin at ca 500 ka because both later *H. heidelbergensis* (a.k.a. archaic *sapiens*) and early *H. neanderthalensis* show many similarities in technology and other aspects of culture, which implies that their common ancestors around that time had similar capabilities. The technological changes included making stone points from prepared cores, and then hafting them onto wooden handles using adhesive peck (which also needs preparation) and special binding materials (Haidle et al. 2015). This complexity and interdependency at least suggests new processes were at work. These tools might therefore have been outside the zone of

latent solutions of the species concerned, *Homo heidelbergensis* (Mithen 1996), since it would (at least with current knowledge) seem unlikely that even a modern human could *independently* rediscover this sequence from scratch. Following this logic, subsequent technologies should have been even more likely cumulative (i.e. as they contained even longer interdependent sequences). While this conclusion is preliminary, so far, no broadly accepted explanation has been offered for the origin of mode-3 technology, which happened when the species had reached a brain size of 1000 - 1200 cm<sup>3</sup>, over twice that of the extant great apes.

Obviously, this does not mean the cumulation process was smooth. Paleolithic archeologists have long recognized the clear uptick in complexity and diversity during the Upper Paleolithic (McBrearty and Brooks 2000; Klein 2008), which is also widely held responsible for the demographic expansion known as Out-of-Africa, which took off after ca 75 ka and led to a massive population increase, largely through the colonization of all continents but Antarctica (Hoffecker and Hoffecker 2017), as well as increased technological complexity (Klein 2008). To Harcourt (2015) this rapid and sustained colonization of unfamiliar regions implies a sudden, dramatic leap in true curiosity in the form of novelty seeking and extensive exploration. Some have even claimed that this process left a genetic footprint (Matthews and Butler 2011; Gören 2016; but see Campbell and Barone 2012).

The last major increase in the rate of technological ratcheting began after the origin of sedentary life and increasingly intensive agriculture at ca. 10 ka (the Neolithic Revolution). Very soon after the Neolithic,

metallurgy arose, followed by an unprecedented rise in complexity of technology and institutions. It is broadly agreed that this steep increase in the rate of cultural evolution was due to the origin of sedentism and the development of ever more efficient agricultural techniques (Scott 2017), including specialization, accompanied by a veritable population explosion and dramatic changes in social organization (Nolan and Lenski 2009; Diamond 2012). We will therefore not pursue the explanations for this last event, but focus on the first two.

### **Modeling cumulative culture**

A variety of factors may favor cumulative cultural evolution. How are we to tie its origin and subsequent changes in its pace to the most relevant variables? Culture obviously relies on innovation and subsequent increases in the frequencies of these innovations in the form of socially induced reinnovation or copying. In cumulative culture, the complexity of a particular innovation in a population is a function of the balance of cumulation through additional innovation or immigration and loss of complexity or even extinction through failure of transmission.

Theoretical attempts to understand this cumulation process follow two broad approaches. The first approach focuses on the fidelity of transmission. Lewis and Laland (2012) exemplify this approach. Pradhan et al. (2012) are similar, but explicitly derive their model from the observed natural history of great ape technology, and we will expand on it here. The model incorporates innovation rates ( $\epsilon$ ) and transmission rates,

with the latter a function of the individual's ability to learn socially ( $\alpha$ ) and the number of tolerant experts and their involvement ( $\kappa$ ). In addition, it takes into account population size ( $N$ ) and life history (mortality rates and the duration of immaturity and thus learning). The goal is to think systematically about how changes in the values of the relevant variables will affect the degree of cumulation, without changes in brain size and thus intrinsic cognitive ability. In the following account, we will use previously unpublished results from this model to illustrate some conclusions (see Pradhan et al. 2012, for full details).

In the Pradhan et al. (2012) model, innovation is favored by larger population sizes and exchange between populations, and by greater individual innovativeness (intelligence, curiosity). Social transmission is favored by longer contact between generations, by population size and by social network structure (tolerance produces a greater number of role models for naïve learners). Social transmission also depends on features of the learners, especially their ability to actually pick up new innovations, i.e. by their ability to actually copy (e.g. to imitate actions and action sequences that are novel to them), and by features of the experts, in particular the degree to which they are actively aiming to pass on their skills (their levels of teaching). Finally, social transmission depends on life history, in the form of mean lifespan, and thus opportunities for social transmission of innovations (each individual is born naïve), and the duration of the immature time window of social learning.

The second approach –was introduced by Henrich (2004). The models, dubbed treadmill models, focus on the fate of a particular skill,



which is transmitted to the next generation, whose members show a distribution of skill levels around the role model's skill level. Learners are assumed to focus on the most skilled individuals for learning, but commit errors when learning, such that the mean skill level will decrease. However, there is variance in the error, which is positively linked to population size, and presumably also to overall complexity (see Andersson and Read 2016). Thus, if population size is large enough, the most skilled individuals in the next generation end up being more skilled than their role models, and skill level will increase. Notice that in these models, which concentrate on the most complex skills, there is no teaching or other processes guaranteeing fidelity of transmission. However, there is a direct link between demography and skill level: that latter goes down in small populations, up in large ones. While we focus on the fidelity approach, we will bring in comparisons with the second where relevant.

## **Explaining the origin and elaboration of human cumulative culture**

We start with the variables affecting innovation and then turn to those affecting social transmission.

### *Innovation: population size and social networks*

Population size can affect innovation in an entirely passive way: if each individual has a particular probability of making an innovation ( $\epsilon$ ), then in a larger population (defined as a collection of individuals that are in contact), more innovations will arise per unit time ( $N \times \epsilon$ ). However, in a

species capable of true social transmission of skill (copying) and where individuals are in contact, once innovations arise in a given population, they can then be passed on and so be retained. This leads to a higher level of cultural complexity (namely when innovations build upon earlier innovations, i.e. the ratchet effect). Fig. 1 illustrates this for the model of Pradhan et al. (2012), where we imposed a maximum level of complexity of three steps of cumulation or ratcheting. Larger population size greatly speeds up the technological cumulation process, not just by favoring the emergence of new innovations but above all by improved retention. Even so, for each set of parameter values, a maximum complexity will eventually be reached, due to time constraints on learning during development. Lewis and Laland (2012) reach the same conclusion in their unbounded model, stressing that fidelity of transmission played a greater role than innovation. However, they also show that the kind of innovation with the strongest effect is trait combination, a source of innovation where two existing techniques are combined into a novel combination. Finally, as we noted above, in treadmill models (Henrich 2004; Powell et al. 2009) cumulative evolution is directly proportional to population size in both directions. Thus, larger populations should have more complex cultures, with no upper limit.

Perhaps surprisingly, the ethnographic evidence for a strong effect of demography is mixed (e.g., Collard et al. 2013; Andersson and Read 2016; Vaesen et al. 2016), and instead suggests that resource pressure or environmental risk may better predict innovation repertoires among foragers. One possible reason is that in a given habitat, with a particular

301 constellation of ecological challenges, even a smaller population may  
302 eventually reach the equilibrium technology level if there is enough time  
303 and no catastrophes, especially when nomadism imposes strict limits on  
304 material culture. A recent study (Fogarty and Creanza 2017) strongly  
305 supports this interpretation, both empirically and theoretically.

306         This implies that demography need not have been a causal factor  
307 while all humans were still fully nomadic foragers, i.e. until well into the  
308 Upper Paleolithic. Indeed, both archeology (Klein and Steele 2013) and  
309 genetics (Li and Durbin 2011) suggest effective population sizes were quite  
310 modest around 75 ka when humans had already developed effective new  
311 technology and began to move far out of Africa (Klein 2008). Thus, there is  
312 little empirical evidence for the proposition that population size can affect  
313 cultural evolution directly when lucky innovations start a positive  
314 feedback loop between innovation and population (cf. Laland 2017),  
315 although all approaches predict it.

316         A more indirect effect of demography may therefore have been  
317 more instrumental. Long-distance contact between groups can create a  
318 much larger social network and thus allow for rare innovations to spread  
319 far and wide (Henrich 2004; Powell et al. 2009). Both the number and the  
320 size of subpopulations as well as the rate of migration between them affect  
321 the cumulation process (Powell et al. 2009). We can use the Pradhan et al.  
322 (2012) model to illustrate the powerful effect of cultural diffusion. We can  
323 once a year randomly pick a single individual in a population of 500 and  
324 increase its technology level by one year. Fig. 2 shows how this can  
325 massively enhance a population's technological complexity. Thus, cultural

diffusion through contact can easily swamp any effects of local population size, in both directions. Such contact with other groups has been shown to be important among extant nomadic foragers, whose visits to other communities allowed them to observe hundreds of experts over a lifetime (Hill et al. 2014). But archeologically, the first unambiguous evidence of long-distance trade and thus such non-hostile contacts between societies is at 200 ka (Blegen 2017), well after the time suggested here as the appearance of the first truly cumulative technology. However, the origin of full-fledged language (Dediu and Levinson 2013) at around 500 ka may have facilitated non-hostile contact between neighboring communities and so facilitated cultural diffusion. Thus, indirect demographic (social network) effects may well have been stronger than actual community sizes or population densities.

#### *Innovation: curiosity*

In addition to external factors such as population size and contact, intrinsic factors may also affect innovation rate. Across species, various studies have found a correlation between relative brain size and the frequency of observed innovations (Reader and Laland 2002). However, this correlation need not reflect a directly causal effect of brain size on innovation tendency, because there may be a major effect of the retention of innovations helped by social learning (van Schaik et al. 2016), which is also far more likely in more encephalized species (Reader and Laland 2002). Moreover, the best evidence concerns survival upon release into

novel regions, and thus need not reflect innovativeness under normal conditions (e.g. Sol et al. 2008).

We raise this more complex interpretation because wild apes show a striking lack of curiosity (novelty seeking plus extensive exploration). Thus, young orangutans are selectively curious, exploring items novel to them only after trusted older experts, initially always their mothers, have handled them (Schuppli et al. 2016). Such targeted exploration is both effective and safe. All wild orangutans strongly avoid any novel items placed in their environments (Forss et al. 2015), as do many other species (Forss et al. 2017). Gruber et al. (2009) showed experimentally that exploration of problem-solving opportunities is also minimal: adult chimpanzees in the wild do not recognize obvious alternative solutions to a problem (obtaining honey from a tree hole), even when the solution is observed, and even if the solution is within reach of individuals that have not had the individual experience to develop functional fixedness (cf. Hanus et al. 2011). Overall, then, the most encephalized species in the wild stand out more by their conservatism than their innovativeness. We therefore suspect that increased brain size need not directly translate into clearly higher innovation rates in hominoids, and thus hominins.

Accordingly, despite decades of intensive field study of great apes, there is indeed remarkably little evidence for the origin of novel innovations, let alone for such that subsequently increase in frequency (e.g. Yamamoto et al. 2008). The natural examples that are well documented are minor variants on existing themes, such as moss sponging rather than the already present leaf sponging (Hobaiter et al. 2014), which may not even

be cognitively distinct to the users. Stone tool use, the only known modern primate technology that left directly recognizable debris in the archaeological record (plant material does not last long in these conditions), has been shown to be old. For instance, Mercader et al. (2007) showed that nut cracking by chimpanzees using stone tools is at least 4,300 years old, and potentially much older, and has fundamentally remained the same since that time (Dean et al. 2014).

Wild apes thus show a remarkable conservatism and lack of curiosity (e.g. van Schaik et al. 2016). This tendency is almost certainly adaptive in that novel items are potentially dangerous and social information, when available, is therefore preferred, especially in species with a long life expectancy (Forss et al. 2017). The same conclusion might well apply to our hominin ancestors during much of human evolution. Many people may find this conclusion surprising, because when they think of apes they have in mind *captive* apes, which are indeed rightly renowned for their innovativeness. In fact, Damerius et al. (2017a, b; see also Forss et al. 2015) showed that captive orangutans are far more curious than their wild counterparts, at least in part because captive orangutans have had extensive contact with humans from a very early age, which unleashed their curiosity. The erosion of the reluctance to explore novelty in captivity (especially when enculturated) indicates that novelty seeking is a latent ability that can be elicited by particular developmental conditions.

Because *modern* humans are often curious, the challenge is to identify when our ancestors became more like captive apes. In the wild the dormant potential is most likely expressed under conditions of great

necessity, when regular subsistence techniques have suddenly become ineffective. This would explain the increase in realized technology shown under environmental risk (Andersson and Read 2016; Fogarty and Creanza 2017), when necessity clearly acts as the mother of invention.

#### *Social transmission: imitation*

One current view holds that great apes largely lack cumulative culture because their copying abilities are not good enough: while they can individually innovate behavior (including tool making and tool use), they seem to lack the motivation and/or ability to copy the styles and forms of others' innovations (Tennie et al. 2018). It is indeed clear that a modest increase in the efficiency of social transmission due to improved social learning (or help in the form of teaching; see below) can produce a steep increase in technology level (Lewis and Laland 2012). Fig. 3, based on the Pradhan et al. (2012) model, illustrates this. Indeed, given that the baseline value for wild great apes learning tool use,  $\alpha$ , is 0.25 at best, it is clear how even a small increase in the efficiency of social transmission can provide a major boost to technological cumulation.

Indeed, it is often argued that cumulative culture requires faithful transmission so as to create a uniform platform that stays intact for long enough for subsequent modifications to happen "on top" (Tennie et al. 2009; Lewis and Laland 2012; Heyes 2018). The key improvement would involve a move away from using social learning mechanisms that are merely socially elicited individual learning (*non-copying* social learning; widespread in the animal kingdom) toward *copying* social learning (which

is then able to transmit *form*, i.e. hierarchical and/or style components of demonstrations – a crucial pre-requisite of the ratchet effect; Tennie et al. 2018). Once copying of actions (imitation) is in place, and especially the copying of *novel* actions (broader range), it can be applied in a broad range of conditions (e.g. communication [itself able to increase fidelity] and tool making and use), and raises transmission fidelity. And while a detailed physical understanding can theoretically allow observers to re-engineer technology (various forms of so-called emulation learning), even here action copying can be of benefit, because actions are hierarchically higher than environmental results (they *cause* these results and thus come first) and also bear an intimate correlation with their results (action A on object X may reliably produce result A), and so the simultaneous copying of both actions and results disproportionately increases fidelity (Acerbi and Tennie 2016). For these combined reasons, action copying favors cultural evolution.

Do great apes copy actions in this way? Evidence for action copying in wild great apes (and, likewise, unenculturated captive apes) is debated, but weak at best (CT et al. unpublished data), whereas *enculturated* great apes, i.e. individuals that grew up with humans and were treated much like human babies are, do show evidence of action copying (Russon and Galdikas 1993; Tomasello et al. 1993; Subiaul 2016), along with the requisite *changes* in brain structure that are required and that resulted from such “training” (Bard and Hopkins 2018; Pope et al. 2018). This indicates that apes can be induced to socially construct the ability to imitate by exposure to rich inputs, perhaps especially numerous novel



450 actions and/or long sequences of actions with unexpected outcomes.  
451 Indeed, Catmur and Heyes (2018) argue that imitation in humans is  
452 similarly constructed during development based on social inputs (i.e. is a  
453 “cognitive gadget”, Heyes 2018)

454         The upshot of this recent increase in our understanding of ape  
455 imitation is that imitation is possibly no longer the magic bullet for the  
456 evolution of cumulative culture. Clearly, the ability to engage in imitation,  
457 including production imitation (*sensu* Byrne 2002), lies – as a potential –  
458 dormant in every great ape, and can be constructed when the inputs are  
459 right or perhaps even if they require it (we postpone asking about the  
460 origin of these complex inputs to the discussion).

461

#### 462 *Social transmission: teaching*

463         In species capable of social learning of copying types, teaching –  
464 social learning with an actively involved demonstrator - provides a major  
465 boost in transmission efficiency (Fogarty et al. 2011; Dean et al. 2014;  
466 Morgan et al. 2015) and perhaps also in the possible complexity of  
467 innovations that can be copied. Teaching in this way is seen in large-scale  
468 human societies (Csibra and Gergely 2011) and, albeit less pervasively,  
469 also in hunter-gatherers (Kline 2014; Hewlett and Roulette 2016), whereas  
470 despite all efforts to detect it, the evidence for great apes is extremely thin  
471 (Hoppitt and Laland 2013; Moore and Tennie 2015). However, (non-  
472 intentional) teaching is common among primates that are cooperative  
473 breeders (Humle and Snowdon 2008; Rapaport 2011). Because teaching  
474 can provide a boost to transmission fidelity, and can initially do so without

requiring the evolution of complex cognitive machinery, it is among the most important drivers of cultural complexity (Tomasello 2009; Pradhan et al. 2012; Dean et al. 2014). Thus, the timing of the origin of teaching may hint at the origin of cumulative technology (Fogarty et al. 2011; Laland 2017). Note however, that teaching should always be split up by the underlying social learning mechanisms (Hoppitt et al. 2008). Here, we are interested in teaching forms that use social learning mechanisms involving copying (which is why we do not elaborate on the occurrences of other, non-copying forms of teaching in the animal kingdom; see, e.g. Hoppitt et al. 2008).

## **Discussion**

When trying to identify the variables leading to cumulative technology, it is generally most profitable to look for changes in the external variables, either the habitat (as driven by the rate and amplitude of climate change: Richerson and Boyd 2000) or other, habitat-driven aspects of the social system, such as the rearing system (van Schaik and Burkart 2010) and environmental risk (Andersson and Read 2016). Above, we suggested that the archeological record does not support increased population size or a positive feedback loop between population size and innovation as the sole cause for the onset of cumulative technology. Of course, it remains possible that a relatively short period of favorable climate pushed up (some) hominin populations, and so gave rise to innovations that raised carrying capacity enough to unleash a positive

feedback loop between population size and innovation repertoires.

However, the lack of clear evidence for a sustained increase in population

size during the Middle Pleistocene does not support this possibility.

Instead, we identified the onset of language-butressed teaching involving

copying of novel actions and, later, curiosity as key variables for the onset

of cumulative culture and its acceleration before Out-of-Africa, respectively

(Table 1).

### *The dawn of cumulative cultural evolution*

Roughly following Tennie et al. (2016), we tentatively pinpointed

the period after around 500 ka to mark the onset of the first cumulative

technology. This suggests that *Homo heidelbergensis* evolved a new

lifestyle. Indeed, around this time or somewhat later (the latter perhaps

due to the incomplete record in most of Africa) the first solid evidence is

found for systematic controlled use of fire (Roebroeks and Villa 2011), and

especially for new technology, including composite tools (Wilkins et al.

2012), the use of throwing spears (Thieme 1997), and the inferred use of

full-fledged language (Dediu and Levinson 2013). This latter factor may

hold the key.

The classic candidate processes to explain the origin of cumulative

culture are high-fidelity copying (especially imitation) and teaching

(Tennie et al. 2009; Laland 2017). We tentatively discounted the limiting

role of imitation since great apes can be led to developmentally construct

the ability (as a “cognitive gadget” sensu Heyes 2018) in conditions where

more complex actions or action sequences must be learned. This leaves

525 teaching (cf. Tomasello 2009; Fogarty et al. 2011). Because teaching  
526 improves transmission and so retention of innovations, it favors increased  
527 innovation capacity whenever innovations enhance fitness. Modern  
528 humans, in addition to silently providing examples and physically shaping  
529 others' behavior (an understudied form of true social transmission), often  
530 rely on language in instruction. Indeed, experiments have shown that  
531 learning to make stone tools becomes far more efficient when verbal  
532 instruction is added to the mix (Morgan et al. 2015; cf. Zwirner and  
533 Thornton 2015). This suggests that effective teaching, especially of  
534 functionally opaque actions that are part of a longer chain and which  
535 require copying for their acquisition, could only become prominent after  
536 language had evolved to a sufficient level of complexity to make this  
537 possible. Once it was in place, correlated evolution between teaching,  
538 imitation and cumulative culture could ensue (Laland 2017).

539       Language did not evolve overnight, and precursors must have  
540 existed (Tomasello et al. 2012). Teaching is more common among  
541 cooperative breeders (Rapaport 2011), and hominins may have become  
542 cooperative breeders and thus more cooperative than extant great apes  
543 (Tennie et al. 2016) well before they invented the prepared core technique  
544 (Hrdy 2009; Isler and van Schaik 2012). The fundamentally prosocial  
545 attitudes toward fellow group members that characterize cooperative  
546 breeding (Burkart et al. 2014) will have favored the evolution of both  
547 teaching and language (Burkart et al. 2018), as teaching is, in essence,  
548 prosocial: Tennie et al. 2009; van Schaik and Burkart 2010). Thus the  
549 combination of teaching and language produced cumulative culture. The

550 plausibility of this model is enhanced by the fact that the external factor  
551 producing the onset of cumulative culture was not a cognitive one but  
552 rather a change in the rearing and social system (van Schaik and Burkart  
553 2010; Laland 2017). Assuming an externally caused increase in cognition  
554 merely moves the question to the source of this increase. However,  
555 cooperative breeding (and, with it, teaching) may plausibly have been  
556 elicited by increasing climate fluctuations (cf. Richerson and Boyd 2000),  
557 because it is known to be favored when productivity declines (Griesser et  
558 al. 2017) and among mammals, is overrepresented in the most  
559 inhospitable climates (Lukas and Clutton-Brock 2017).

560         This leaves the question how the adoption of language-buttressed  
561 teaching may have led to greater innovativeness in our ancestors. Once  
562 effective teaching exists, selection will favor individuals who acquire the  
563 local population's set of innovations as fully and rapidly as possible.  
564 However, this selection also automatically improves individual or asocial  
565 learning skills (van Schaik and Burkart 2011; Heyes 2012), leading to  
566 better and faster innovation, which in turn favors the developmental  
567 construction of imitation (see above). These mutual positive influences  
568 create a positive feedback loop, leading to coevolving innovation and  
569 imitation abilities. This loop also includes changes in life history (e.g. by  
570 slowing down development and expanding the learning period to beyond  
571 sexual maturity) and brain size. This process may bring about a quantum  
572 leap in the complexity of technology because teaching (because of its  
573 highly increased fidelity) allows naïve individuals to bypass the historical  
574 sequence of innovation steps that led to the current, complex technique

and simply skip to the current technique. Such shortcutting also increases the likelihood that young individuals make additional innovations (often by mistake; cf. Henrich 2004; Eerkens and Lipo 2005) that improve upon the existing technique.

Overall, then, the process that produced both effective language and teaching in a coevolutionary process is the most plausible candidate for the origin of complex and truly cumulative material culture in hominin evolution.

#### *The origin of curiosity*

The idea that a gradual increase in cumulative culture in Africa was the root cause of the rich and complex material culture of the humans that appeared in Europe at ca 42 ka (McBrearty and Brooks 2000) suggests no step-wise change in the cumulation process. Nonetheless, many suggest that some major new factor underlies by the rapid, sustained Out-of-Africa dispersal that began around 75 ka, and by the continuing rapid increase in complexity since then. As discussed above, a sudden increase in novelty seeking or curiosity was recently suggested as the key underlying change.

We noted that in great apes, curiosity can be elicited even when it normally lies dormant. This idea lends greater plausibility to the novelty-seeking hypothesis, because the existence of a phenotypic switch to turn on curiosity enables rapid responses during a brief period in which regular techniques have become ineffective. If the onset of curiosity had required genetic responses, local populations would probably have gone extinct well before they could respond adaptively. It is also possible, as suggested by

the geographic gradient in variants of the dopamine receptor gene (Matthews et al. 2011; Gören 2016), that selection on the suppression of previously maladaptive curiosity was relaxed, allowing the variant alleles of the dopamine receptor gene to spread during to the dramatic range expansion.

Obviously, future work is needed to evaluate this radical idea, in particular with respect to the event that elicited this shift in some local population(s). For example, the Toba eruption may not have led to a population collapse in Africa and adjacent regions, as previously claimed (Ambrose 2003), but it may have produced a brief ecological crisis, serious enough to lead some individuals to lose their neophobia and try out unusual resources or habitats.

### *The Neolithic revolution*

The origin of agriculture was preceded by a period in which foragers in some regions became more sedentary. Sedentary foragers have more, and more complex, technology than nomadic ones (Torrence 2001). Agriculture added another major impetus to expand technology, partly made possible by specialization, but also led to a strong increase in population size and contact between societies through trade or conquest (Scott 2017). Large populations produce more innovations passively (by greater numbers or greater diffusion), by allowing specialization, or by producing wars and ecological crises that necessitated innovations (Fogarty and Creanza 2017). In this phase, clearly the feedback loop between population size, social exchange and the accompanying cultural

diffusion had become major engines of cumulative culture, with seemingly open-ended outcome (Laland 2017).

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## **Conflict of Interest**

The authors declare that they have no conflict of interest.



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894

## **Figure Captions**

Fig. 1

Effect of population size (N) on time taken to reach complex technology  
(here constrained to maximum level 3) when starting from scratch.

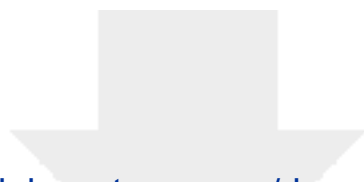
Detailed methods provided in Pradhan et al. (2012)

Fig. 2

Effect of diffusion on ratcheting. Diffusion was simulated by increasing a  
single randomly picked individual's technology level by 1 in any given year,  
in a population of 500 individuals, constraining the maximum technology  
level at 6 (where  $\kappa=2$ ,  $\alpha=0.4$ ; for details see Pradhan et al. 2012)

Fig. 3

The time needed to reach a complex level of cumulative technology, as a  
function of the efficiency of social transmission, for realistic values of great  
ape sociability ( $\kappa=2$ ) (for details see Pradhan et al. 2012)



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